

HYBRIDIZATION AND SEASONAL SEGREGATION IN TWO RACES OF A BUTTERFLY OCCURRING TOGETHER IN TWO LOCALITIES

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The yellow and orange butterfly, *Colias chrysotheme*, exists in the form of two complexes known as the orange-race and the yellow-race (Hovanitz, 1943a; 1943b). These races have different geographical distributions but overlap over a tremendous territory from the Sierra-Cascade divide in western North America to the Atlantic ocean in the east and from southern Canada in the north through Mexico in the south (Hovanitz, 1943c). Each race usually occupies a different ecologic niche so that nearly pure populations of each may be found in this area as well as outside the zone of overlap. In certain localities, however, the same ecologic niche is partly occupied by both races, resulting in considerable hybridization between them.

Two localities where the races occupy the same niche for the most part were analyzed from 1941 to 1943 in order to study the behavior of each in relation to its environment, and to get an indication of the extent of hybridization between them. These places were at Mono Lake Valley, Mono County, California, and at Round Valley (near Bishop), Inyo County, California. Their positions are indicated on a map (Hovanitz, 1943d); they are just east of the Sierra Nevada in the western Great Basin.

The Seasonal Distribution of Adults

Orange butterflies are present throughout the entire warm season of the year at both Round Valley and Mono Lake. It is easier, however, to get a good sample in midsummer as compared with early spring or autumn. The abundance of orange adults apparently is at a minimum at each end of the growing season and at a maximum in midsummer.

The yellow butterflies at Mono Lake are more irregular in seasonal distribution than the orange (Fig. 1). The 1941 samples (Table I) show a high relative frequency of yellow to orange in May, and then a complete drop to none present at all in June. A rise to a second maximum in late July is apparent with a gradual drop again to none at all in September. Early in October there is a third maximum. This suggests three distinct broods per year at Mono Lake with an elapsed egg, larval and pupal development time of two months between each. This time compares with a development rate of three to four weeks at a constant laboratory temperature of 25° C. Mono Lake has a rather low air temperature, especially at night; in the day time, the direct radiation from the sun is the primary source of heat.

The 1942 samples at Mono Lake show much the same seasonal distribution.

The first adult flight was apparently not observed; it is probably very short in duration. The 1942 samples were obtained at monthly intervals rather than semi-monthly as in 1941; therefore, the chance of missing a short adult flight is increased. The second and third broods of 1942 are to be found indicated in the figure a few weeks earlier than in the preceding year. As 1942 was a warmer year for Mono Lake than was 1941, an earlier start in larval development in the spring, with a consequent shift forward in the successive broods, would thus be expected.

The two 1940 samples at Mono Lake show no yellow butterflies present at all. Therefore, it would appear that they were obtained in a yellow interbrood period (Fig. 1).

The frequency at Round Valley does not follow this sequence of events (Fig. 1). Neither the 1941 nor the 1942 samples show any correlation with those

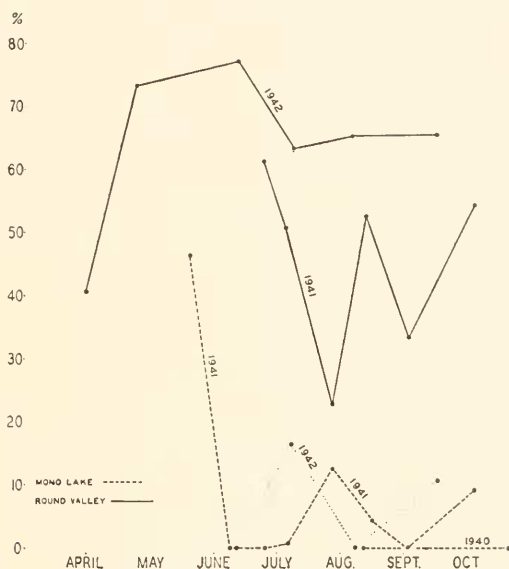


FIGURE 1. Frequency of yellow to orange butterflies at Mono Lake and Round Valley, California, throughout the season. Note the complete absence of yellow at certain times at Mono Lake as compared with Round Valley.

of Mono Lake (Table I). This shows the complete lack of intermixing between the two places though they are only fifty miles apart. The 1941 Round Valley curve is high in late June (60 per cent yellow) and drops to a low in late July (25 per cent yellow). A rise occurs in mid-August (53 per cent), with a subsequent drop again the first of September (34 per cent), and then a last rise in early October (55 per cent). If these fluctuations represent successive broods not completely separated one from the other, then there are many more generations present per year at Round Valley than at Mono Lake. This would be expected considering the warmer climate at the former place (Round Valley is at an elevation of 4500 feet and Mono Lake at 6500 feet). Latitudinal differences in brood number per year parallel these altitudinal ones. There are three generations per year near Washington, D. C. (and Mono Lake), two generations near Hanover, N. H. (and

central British Columbia) and one generation in Alaska and Yukon Territory. At Round Valley there are probably four or more.

The 1942 samples are more extensive at Round Valley than are those of 1941 (Table I). There is a low of yellow (40 per cent) in early spring, rising to a high within the month of 75 per cent and later 79 per cent, with a rather constant frequency of 65 per cent yellow the remainder of the year. This curve shows little evidence of a series of broods or generations during the year. At the rather high temperatures prevailing in the valley during the summer (around 40° C.

TABLE I

The frequency of the yellow-race as compared with the orange-race butterflies at Mono Lake and Round Valley, Calif. Standard errors are used in this and the other tables. The "many" is not included in the figures of totals but indicates the presence of yellow alone.

Date	Round Valley		Mono Lake	
	% yellow	N	% yellow	N
<i>1940</i>	—	—	—	—
Aug. 11	—	—	0.0	105
Oct. 20	—	—	0.0	46
<i>1941</i>	50.50 ± 2.89	299	5.84 ± 0.63	1,387
May 4	many	many	—	—
May 19	—	—	46.27	75
June 8	—	—	0.0	91
June 24	61.19	134	0.0	70
July 5	50.82	61	0.89	678
July 26	22.92	48	12.66	237
Aug. 15	52.63	19	4.21	95
Sept. 2	33.33	15	0.0	20
Oct. 4	54.55	22	9.01	121
<i>1942</i>	65.96 ± 1.50	987	10.68 ± 0.88	1,236
April 1	40.82	49	—	—
April 25	74.55	110	—	—
June 12	77.14	140	0.0	many
July 7, 8	63.70	540	16.16	396
Aug. 6, 7	65.22	69	0.0	434
Sept. 16	65.82	79	10.67	406
1940-41-42	62.36 ± 1.35	1,286	7.68 ± 0.51	2,774

during the day, and fluctuating but not very cool at night), the succession of generations would be at about one month intervals. The samples were made at this interval of time, so it is quite possible that the sampling periods coincided with the periods of adult emergence. Were this the case, the results would show a rather constant seasonal frequency. On the other hand, it is possible that the variations in development rate between individuals owing to micro-temperature differences in the locality have completely eliminated the inter-brood population minima. This has been shown to be partially true for the second and third broods in the vicinity of Washington, D. C., as well as for New York state. In these

places, only the breaks between broods one and two are clearly defined by the absence of adults.

A higher frequency of yellow at Round Valley than at Mono Lake, at all times, is apparent (Fig. 1). Several factors combine to create this difference: (1) more larval food is present at Round Valley (*Trifolium*), (2) Round Valley is farther ecologically from the source of the migrant orange-race individuals (San Joaquin Valley), for these are more likely to stop in the mountain meadows than to proceed through the desert to Round Valley. The frequency of yellow is given as compared with orange. When the orange frequency goes down, the yellow will appear to rise in the curve. (3) The longer and warmer growing season at Round Valley gives more time for the resident population size to be built up. This has been shown elsewhere by the increased numbers of individuals in the second and third broods at Washington, D. C., and New York as compared with the first spring brood.

TABLE II

The frequency of intermediates in the mixed population of orange and yellow races of Colias chrysotheme at Round Valley, California. (The total given in Table I does not include intermediates; hence, it is smaller than that given here.)

Date	1941	N	Date	1942	N
	% intermediates			% intermediates	
May 4	—	many	April 1	10.91	55
June 24	14.65	157	April 25	7.56	119
July 5	11.59	69	June 12	14.15	163
July 26	9.43	53	July 7, 8	6.08	575
Aug. 15	32.14	28	Aug. 6, 7	6.76	74
Sept. 2	0.0	15	Sept. 16	12.22	90
Oct. 4	0.0	22	1942	8.27 $\pm$ 0.84	1,076
1941	13.08 $\pm$ 1.82	344	1941-42	9.44 $\pm$ 0.78	1,420

A higher frequency of yellows at Round Valley in 1942 as compared with the 1941 samples is also indicated. The latter samples were obtained in a mixed alfalfa-red clover field at the periphery of the large meadow which constitutes the primary ecologic niche for the yellow-race. The 1942 samples were made at a different field one mile from the latter (containing alfalfa, red-clover, white clover and native perennial clovers) in the center of the meadow. This field would be in the midst of the population for the yellow-race whereas the former field is on the periphery. For the migratory orange-race (Hovanitz, 1943d), no part of the meadow would constitute a population center. The higher frequency of yellow in 1942, therefore, can be accounted for by this change in position of the place sampled.

Hybridization Between the Races

Genetic data on crosses involving the races and on progeny from wild intermediates between the races indicate that crossing is easily possible and occurs

frequently (Hovanitz, 1943b). Also, the indications are that there is no genetic sterility between the races. The F_1 is an exact intermediate of a light orange color; F_2 and backcrosses give the range of intermediates expected on a multiple factor distribution of genes.

The range of colors from the parental types through the intermediates is given in a range from yellow to orange of 1 to 10. From genetic results, it is known that grades 1 and 2 are pure parental types, breeding true for the yellow race. In the pure populations of orange race, there is a range of yellow to orange from 1 to 10 but from about 1 to 7 or 8 these are exceedingly rare (Hovanitz, 1943e). Therefore, grades 8 to 10 in the males and 7 to 10 in the females are considered as "parental types" for the Round Valley population. It is understood that grades 7 or 8 may be intermediates or that some lower grades may be parental types but that these will be insignificantly small.

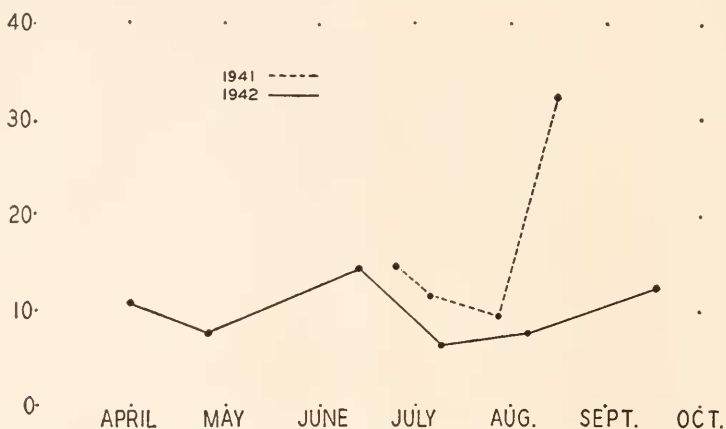


FIGURE 2. Frequency of intermediates between yellow and orange in the population at Round Valley, California, during the two years 1941-42.

On the basis of grades 3 through 7 in the males and 3 through 6 in the females, the frequency of intermediates in the Round Valley populations have been calculated (Table II). It is seen that there is but little seasonal change in the abundance of intermediates (Fig. 2). A high of 30 per cent in August 1941 is possibly a result of the small sample size. An average of about 10 per cent intermediates is usual.

Range of Wild Intermediates

The statistical consequences of continued interbreeding between the orange and yellow races should be a single race combining the characteristics of each parental type. But the two races have maintained their primary discreteness after more than 70 years of such interbreeding, and probably for many centuries (Hovanitz, 1943b; 1943c). Were the interbreeding only of very recent origin, the hybrid range would show a very high frequency of F_1 intermediates (grades 5 or 6) and a lower range of F_2 , F_3 and backcross intermediates (grades 3-4, 7-8). The data on wild individuals (Fig. 3) do not show this higher frequency of F_1 to

any great extent. The female curve may be masked by the normally low orange female grades. The male range shows a somewhat higher frequency of grade 5 than the other intermediates. The lack of the F_1 intermediates compared with

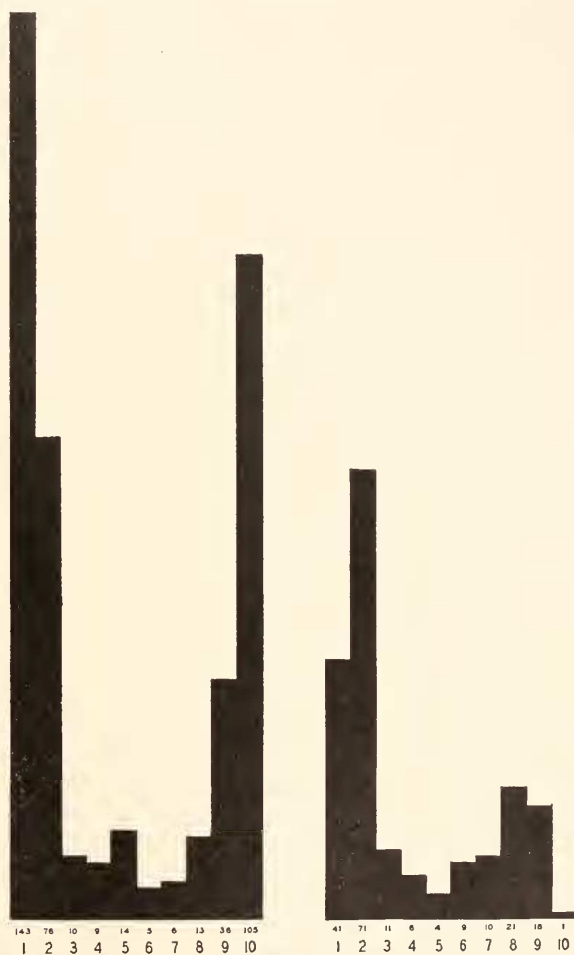


FIGURE 3. Histograms showing the range of variation in the intermediates between the orange and yellow races at Round Valley, California, 1941-42. Male on left and female on right. The smaller numbers represent the numbers of individuals in a given class and the larger represent the grade or class of intermediates.

F_n intermediates may be due to many factors of which a general lower viability seems to be the most likely (Hovanitz, 1943b).

DISCUSSION

The data on the existence of the two races of *Colias* living in the same locality suggest how ecologic and physiological differences can be maintained in units

which may be called species. The races are not here called species for some genes are easily and often interexchanged (Hovanitz, 1943b). However, other genes are not effectively segregated in this way. This suggests that the significant gene complex characterizing each race and giving it individuality is not broken down in hybrid crosses.

Since the color difference separating the races is a multiple factor one and these factors are segregated independently of the basic complex, it might still be expected that a complete intermediate population would be produced, separated only by the non-visible basic complex. The reason for this lack of complete blending of characters probably lies in a combination of the following conditions:

(a) Sexual selection (Hovanitz, 1943b) may prevent sufficient intercrossing to be effective.

(b) Eggs genetically determined to be yellow-complex laid on alfalfa will later result in sterile adults or the subsequent larvae may die; also the reciprocal on red clover (Hovanitz, 1943; 1943b).

(c) The intermediates of all types are probably less viable than the parental types and many of them will be sterile on the food plant upon which they feed (Hovanitz, 1942; 1943b).

(d) The diapause associated with the one complex (Hovanitz, 1942, 1943b) tends to keep the races ecologically separated.

(e) The supplementary color genes of each normal type probably act better in unison with the basic complex than any intermediate segregation of genes.

(f) The different ecological niche occupied by the food plants necessary for each complex aids in preventing hybridization (Hovanitz, 1943c).

Summary

1. Two localities where the two races of *Colias chrysotheme* occur together are described (Mono Lake and Round Valley, Calif.).

2. In these places, the yellow-race has definite broods during the season. The orange race apparently does not.

3. The yellow-race has more seasonal generations when a population is at a lower elevation (Round Valley) than at a higher elevation (Mono Lake). This compares with latitudinal differences of the same type.

4. The two localities are 50 miles apart, but show no correlation in seasonal generations.

5. The yellow-race generations at the higher elevation are separated by inter-brood periods with no adults. At the lower elevation, the generations merge one into the other.

6. Hybrid intermediates are present at one locality rather constantly at a frequency of about 10 per cent.

7. The range of color intermediates is not trimodal, but a U-shaped curve. This is probably due to a low viability of the F_1 . A trimodal curve is expected under conditions of very recent hybridization and all intermediates with long-time hybridization.

8. Several reasons are given to account for the lack of complete blending between the races after years of hybridization.

Acknowledgments

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LITERATURE CITED

- HOVANITZ, W., 1942. The biology of racial or species differences in *Colias*, *Bull. Ecol. Soc. Amer.*, **23**: 68 (Abstract).
- HOVANITZ, W., 1943a. The nomenclature of the *Colias chrysotheme* complex in North America. *American Museum Novitates* (in press).
- HOVANITZ, W., 1943b. Genetic data on the two races of *Colias chrysotheme* in North America and on a white form occurring in each. (Awaiting publication.)
- HOVANITZ, W., 1943c. The ecological significance of the color phases of *Colias chrysotheme* in North America. *Ecology* (in press).
- HOVANITZ, W., 1943d. The distribution of gene frequencies in wild populations of *Colias*. *Genetics* (in press).
- HOVANITZ, W., 1943e. The pattern elements of the North American *Colias* of the *chrysotheme* group. (Awaiting publication.)

